Notes on the anatomy of Sesban macrocarpa Muhl.*

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(WITH PLATE 34)

Sesban macrocarpa was first described by Muhlenberg in 1818; later, Pursh changed the generic name to *Sesbania*, which form is used by some authors. The species under consideration is the only representative of the genus known in North America, although there are a number in other parts of the world in warm or tropical regions. *Sesban macrocarpa* is one of the annuals which flourish under the conditions that exist in Arizona and the southwest in general, and further south to Central America, although it is known in the eastern section as far north as Pennsylvania. It is placed in the Papilionaceae near *Robinia*, *Astragalus*, etc., in the tribe Galegeae.

Before going into details of the anatomical structure of the plant in question the following review of the anatomical features common to the Papilionaceae will be of interest. The characteristics common to these forms are: † (1) ducts with simple openings, (2) simple pitted wood-prosenchyma, (3) lack of crystal glands, and (4) scarcity of the usual one-celled hairs, (5) ducts filled with brown albuminous substance, (6) hairs which usually consist of one row of cells having one or more short basal cells and one long end-cell, besides (7) excretion of calcium oxalate in the form of staff-like crystals. As the other characteristics are not common to all species, they will not be considered here.

The material used was chiefly raised from seed at the New York Botanical Garden. That from which most of the work was done was fully mature, having flowered. The plants all averaged about the same height, the particular one studied being 105 cm. in length. In order to facilitate orienting the sections, the plant was cut into seven lengths, successively shorter, and the parts were

* Britton, Manual of the flora of the Northern States and Canada, 550.

† Solereder, Anatomie der Dicotyledonen, 288.

mapped out on paper. In this way any section could be cut and its position in the plant ascertained and recorded. Microtome sections were prepared by embedding in paraffin, this method being found suitable even for the older, tougher portions when the harder paraffin was used.

The general structure of the stem was determined by a transverse section at 5 cm. from the tip. This showed 39 definite open collateral bundles arranged in a circle about a central cylinder of pith (FIGURE 1). These were enclosed by a stereome ring separated from the cortex by an endodermis. To determine the changes which had taken place in the development of the stem, a section was taken just above the root (FIGURE 3). Here the bundles had enlarged considerably, forming a complete woody cylinder by the growth of interfascicular cambia, and not by the interpolation of new bundles; the width had increased from 67.8 μ to 2.36 mm. The first evidence of a complete woody cylinder appeared at 88.5 cm. from the base, or at 16.5 cm. from the tip. Another change was in the broken appearance of the stereome, which at 17 cm. from the base showed 44 groups, giving evidence of the inability of these cells to stretch with the growth of the stem in circumference. Besides this a superficial periderm had formed, just above the roots, of six or seven layers in thickness. In several places where wounding had occurred it was deep enough to cut off a portion of the stereome. Very prominent, because of their brown color, were cells filled with tannin, occurring in the cortex, leptome, and pith. In the cortex the tannin filled separate cells without particular order, but in the leptome long ducts, usually three to each bundle, formed a ring concentric with the epidermis, stereome, and cambium. Besides this, single ducts appeared in the periphery of the pith at the base of the large bundles (see FIGURE 2). As the general plan of the plant has been given, the separate elements will now be considered in detail.

The pith, constituting the central cylinder of the stem, was formed of more or less spherical cells, the lignified walls of which were very delicately pitted. In the older stem the cells at the periphery contained considerable starch. The diameter of the pith averaged thirty-nine cells throughout, the increase in the size of the cells causing the enlargement in the diameter of the stem.

The hadrome elements of the bundle varied according to the age of the stem. In the younger sections the annular and spiral ducts only were lignified. In the older portions, the libriform and medullary ray cells formed by far the main percentage of the woody cylinder. The ducts were typical, comprising the annular, spiral, reticulated, and pitted. In the latter the edges of the pits were slightly thickened. They had a very large lumen averaging 71.85 μ in width with a heavy wall of 3 μ in thickness, in contrast to the spiral and ring ducts which measured 28.2 μ across their lumen, with a wall 3 μ thick also. On the innermost edge of the bundles were ducts which differed from the regular annular ring ducts in having lateral lignified circular thickenings. In some sections they appeared like distorted annular ducts, in others, the openings were decidedly lateral and showed no distortion. The long pointed libriform cells averaged to have a wall of 1.5 μ and lumen of 26.1 μ in the older parts. The walls were strongly lignified and but slightly pitted by oblique slits. The parenchyma cells surrounding the base of the bundles became lignified only in the older stem. There was little wood-prosenchyma, but what there was contained starch.

Of particular interest in the study of any Galegeae are the medullary rays in tangential section. Although these plants have no common anatomical character, still three groups have been found whose differences lay in the medullary ray construction.* In cross section in this species, they were one cell wide, had pitted walls, and were filled with starch in the older stem. In radial section they appeared rectangular in shape, forming long horizontal rows, a characteristic of the Papilionaceae and of the Caesalpiniaceae. Some rows comprised taller cells than others, which is true, too, of *Amorpha*, *Indigofera*, and *Psoralea* of the Podalyrieae.† In the younger sections the cells were found to be taller than those in the older parts. The story-like appearance of the cells in the horizontal layers was pointed out by von Höhne and verified by Saupe as occurring mostly in the Papilionaceae, also in the Caesalpiniaceae. In tangential section, the cells form long columns one cell wide, except that in some places, being two

* Saupe, Flora 70:303. 1887.

† Saupe, *loc. cit.* 303.

cells in width and of irregular shape, they marred the otherwise "story-like" appearance.

The cambium ring separating the woody cylinder from the outer leptome mass, varied from three to seven layers according to the age of the plant (FIGURE 6). The leptome with its long sieve-tubes and companion or cambiform cells, was cut off on its outer edge. The sieve-plates were visible only after being stained with Delafield's haematoxylin or with methylene blue. Besides the ordinary transverse oblique plates, twin sieve-plates (FIGURE 7), and a number of lateral ones were found (FIGURE 5). This may be peculiar to this particular species, for no mention is made of this point in the various Leguminoseae which hitherto have been examined.

Scattered throughout the leptome portion, in the older stem, especially near the root, were single spindle-shaped cells or groups of them, more or less sclerenchymatous in character. Their outer wall was lignified, whereas their inner more or less gelatinous or mucilaginous lining consisted of cellulose.* This cellulose lining was quite separate from the wall, as the plant had been in alcohol. There was evidence, in the portion just above the root, that these fibers migrate to the outer edge of the leptome and combine to form the stereome. These cells were most abundant in the root, forming the mechanical tissue in the center in the leptome.

The stereome, formed of long thick-walled lignified cells, 1.807 mm. long, with walls 4.6 μ thick and a lumen of 6.25 μ, pectinated to form a tough fiber of considerable strength. In India, *S. aculeata* Pers. is especially cultivated for its fiber,† from which fishing nets are made. We are told that it is tough and durable, but on account of its shrinkage when wet, is not suitable for ship's cordage. In the younger portions of the stem, the stereome was thin-walled, not being lignified until one reaches a point 22.7 cm. back from the tip, or at 82.8 cm. from the base. After lignification set in, the walls began to thicken (FIGURE 8) and became more rigid. As the circumference of the stem

* Tschirch, Angewandte Pflanzenanatomie 1: 295. Chloriodide of zinc stained the lignified walls yellow, and the cellulose red-violet.

† Maiden, Some Australian vegetable fibers, Agri. Gaz. of N. S. Wales, Misc. Pub. 550: 8. 1902.

increased, the stereome, unequal to the strain, split up into masses (FIGURE 3). At a point 20 cm. from the root, it showed forty-four groups. But just above the roots were only fourteen groups, the number of cells composing each being considerably less than higher up in the stem. But added to these and serving as mechanical tissue were the scattered fibrous cells with the cellulose lining and lignified walls, or bast fibers,* which, as mentioned above, formed the transition stage between the mechanical cells of the root and stem.

Enclosing the stereome was a well-defined endodermis (FIGURE 4). In transverse section the cells were longer than they were wide. This endodermis was not constant throughout the stem. It was very definite in the younger portion, but was lacking in the old. The amount and relation of the starch to the sheath varied in the different sections. At a point 94.8 cm. from the base the starch was confined to the endodermis, where it occurred plentifully. Ten cm. lower, hardly any starch appeared. A cross section taken at 73 cm., or 11 cm. lower, showed very few starch grains scattered in the endodermis. Still lower down, or at 57 cm., the amount of starch in the endodermis was somewhat greater; while at 40.5 cm., no starch was found in the sheath, but considerable in the leptome, some in the medullary rays and some in the periphery of the pith. Still older portions showed the endodermis lacking starch. But in the leptome, in the medullary rays and in the periphery of the pith, there was a great abundance of it. Therefore the amount of starch varied according to the age of the stem. In the young or actively growing region practically none or very little starch was stored, whereas in the older portions large quantities were kept for reserve material until the time for fruiting.

According to Solereder† one often finds as characteristic of the Papilionaceae, glandular cells having a wide lumen and containing brown albuminous substance. For a long time these vessels were considered laticiferous, but the researches of Trécul‡ showed conclusively that the contents were tannin. He classifies

* Tschirch, Angewandte Pflanzenanatomie 1: 295.

† Solereder, Anatomie der Dicotyledonen 288.

‡ Trécul, Compt. Rend. 60: 225. 1865.

the principal ways that the tannin is found to occur in the plants. For *Sesban* he states that it "has tannin-like latex vessels in the external bark, under the phloem and among the pith." The species under consideration, however, had tannin in the cortex, in the leptome, and at the base of the bundles in the periphery of the pith. In the preserved condition in which this plant was studied, the cells containing this secretion appeared brown and granular and were very noticeable under the microscope. The test used for their determination was as follows: The sections were placed in concentrated aqueous solution of copper acetate for three days, and then were treated with a 20 per cent. solution of ferric acetate for a few minutes. The tannin present became greenish blue. In the cortex the tannin cells appeared without any particular order, but in the leptome long ducts had been formed which were quite regularly placed, usually three to each bundle (FIGURE 3). The cross-walls of the ducts were missing, but slight traces of their former position were observed in several places as projections from the wall into the lumen.* Researches of Avetta, Borzi, Baccarini, and Weyland show them to be syncytic in nature.† The tannin cells, themselves, were cylindrical structures, slightly constricted in the center, fitting end to end, averaging 28.16 μ long and 1.76 μ wide in the old stem.

The collenchyma forming a definite ring of three to five layers was interrupted by an aerenchyma (FIGURE 4) of more or less spongy tissue throughout the length of the stem. This was lacking in the root. In *Sesban aculata* Pers. and *Sesban marginata* Benth.,‡ however, a considerable aerenchyma was developed in place of cork in the roots, which functioned as floating tissue.

The cells forming the epidermis appeared polygonal in shape when viewed from above. The stomata were of the usual type, and were surrounded by four neighboring cells. The number of stomata varied considerably; in one strip of epidermis with an area of 7.5 sq. mm. at a point 40 cm. from the base 6, only, were found, while in a smaller piece of 4.7 sq. mm. at 14.7 cm., 22 stomata were present. No hairs of any kind were present.

* Meyen, Ueber Secretions-organe der Pflanzen, 47. Berlin, 1837.

† Solereder, Anatomie der Dicotyledonen, 294.

‡ Scott & Wagner, Floating roots of *Sesbania aculeata*. Ann. Bot. 1: 301–314. 1888. Also Schenck, Aerenchym. Jahrb. Wiss. Bot. 20: 554–557. 1889.

The structure of the root next claims our attention. The plant examined had a well-developed primary root with a thick mass of secondary ones, upon which nodules had formed. Examination of the root of a seedling showed it to be of the radial tetrarch type, the bundles enclosed by pericambial and endodermal layers. As in most Papilionaceae, there was a common meristematic zone extending across the plerome and periderm areas.* An older root showed the bundles meeting in the center, and the leptome pushed out until it formed a ring about the central woody cylinder. The bundles were formed of libriform cells and pitted ducts, but there were no ring ducts. Many of the ducts had cross-walls formed of a fan-like radiating structure† or of ladder-like construction. In this respect the root differed from the stem and from Leguminosae in general, that is, in having simple openings between ducts, as mentioned at the beginning. The medullary rays, too, showed some variation, in being from one to three cells wide. On entering the leptome area, they broadened considerably, becoming wedge-shaped. As in the stem, the cells were filled with starch. The leptome was well developed. The cells contained starch, and were interrupted in a few places by tannin ducts. Scattered in the leptome was a great number of stereome fibers, having lignified walls and a cellulose lining, being of the same kind as occurred in the stem above the root (FIGURE 9). The libriform cells, throughout the center and towards the edge of the hadrome, were of like construction. We are told that the appearance of this "3d membrane" among libriform cells is an irregular one.‡ They showed most prominently after treatment with chlor-iodide of zinc, the lignified walls becoming yellow, and the cellulose lining or "3d membrane" (Tschirch), a red-violet.

The leaf (FIGURE 10) showed the usual dorsi-ventral structure. Weyland § summed up the characteristics in his researches on the Galegeae, one of which was *Sesban.* Examination of the leaf of *S. macrocarpa* showed an agreement in all the details. The stomata appeared on both sides of the leaf, but were somewhat

* De Bary, Comparative anatomy of phanerogams and ferns, 12. [Eng. Trans.]

† "Gefächerte" prosenchyma-cells found by Saupe in species of *Sabinea* and *Sophora;* Solereder, *loc. cit.* 311.

‡ Tschirch, Angewandte Pflanzenanatomie 1: 298.

§ Weyland, Bull. Herb. Boiss. 1: appendix 3. 1893.

sunken owing to the papillose character of the epidermal cells. The neighboring cells, three or more, were arranged in no particular order. Epidermal hairs and glandular cells were lacking, the latter often being found among the Galegeae. The leaf-bundles had no sclerenchyma sheath, but lay embedded in the mesophyl. A few crystals of calcium oxalate were found in the bundles. The palisade parenchyma of two layers was rich in chlorophyl; some of the cells, however, were full of tannin. The spongy parenchyma, below, was two-layered, many cells of which also contained tannin.

The seeds of this plant were invested by an unusually hard resistant seed coat, which refused to split after the usual soaking, except for a very small percentage. Heroic measures were then resorted to. The seeds were put into boiling water and boiled for a minute or a trifle more. After this treatment every one sprouted.

Very little anatomical work has been done upon this genus. The tannin-ducts have been examined by Trécul, the leaf by Weyland, and the floating roots by Schenck and by Scott and Wagner, all of which have been referred to in the preceding pages.

In summing up, therefore, we find in *Sesban macrocarpa* the commonly recognized anatomical characters of the Leguminosae, except that some of the ducts in the roots have fan-like cross-walls in place of simple openings. As for the further characteristics of the Papilionaceae, we find that *Sesban macrocarpa* has the tannin-ducts, but wholly lacks hairs of any kind. As for the calcium oxalate secretion, it was found only in the leaf-bundles. Of special interest may be mentioned the lateral and twin sieve-plates, lateral openings in the annular ducts, the bast or stereome and the libriform fibers having the third membrane, and the resistant coat of the seeds, besides the disappearance of the endodermis in the old stem.

The study of *Sesban macrocarpa* was carried on in the Barnard Botanical Laboratory, under the direction of Professor Herbert M. Richards, to whom his student gratefully acknowledges her appreciation of his help and interest. The original material and seeds were kindly supplied by Dr. D. T. MacDougal of the Carnegie Institution of Washington, to whom the writer wishes to express her thanks. Thanks are due also to Miss Alice A. Knox for her

trouble and work in the sprouting and growing of the seedlings for examination.

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Explanation of plate 34

FIG. 1. Transverse section of stem near tip, showing separate bundles; × 8.

FIG. 2. Detail of fig. 1. *d*, ducts; *t*, tannin; × 39.

FIG. 3. Transverse section of stem at 21 cm. from base, showing complete woody cylinder of 39 bundles; *c*, cambium; *epi*, epidermis; *lept*, leptome; *p*, pith; *st*, stereome; *t*, tannin; × 8.

FIG. 4. Transverse section of stem at 40.2 cm., showing the aerenchyma; *aer*, air space; *col*, collenchyma of 4 layers; *end*, endodermal sheath bordering *st*, stereome; *t*, tannin duct in leptome tissue; × 55.

FIG. 5. Longitudinal section of leptome with lateral sieve-plate, *l. s. p.*; *c. w.*, cell wall; × 318.

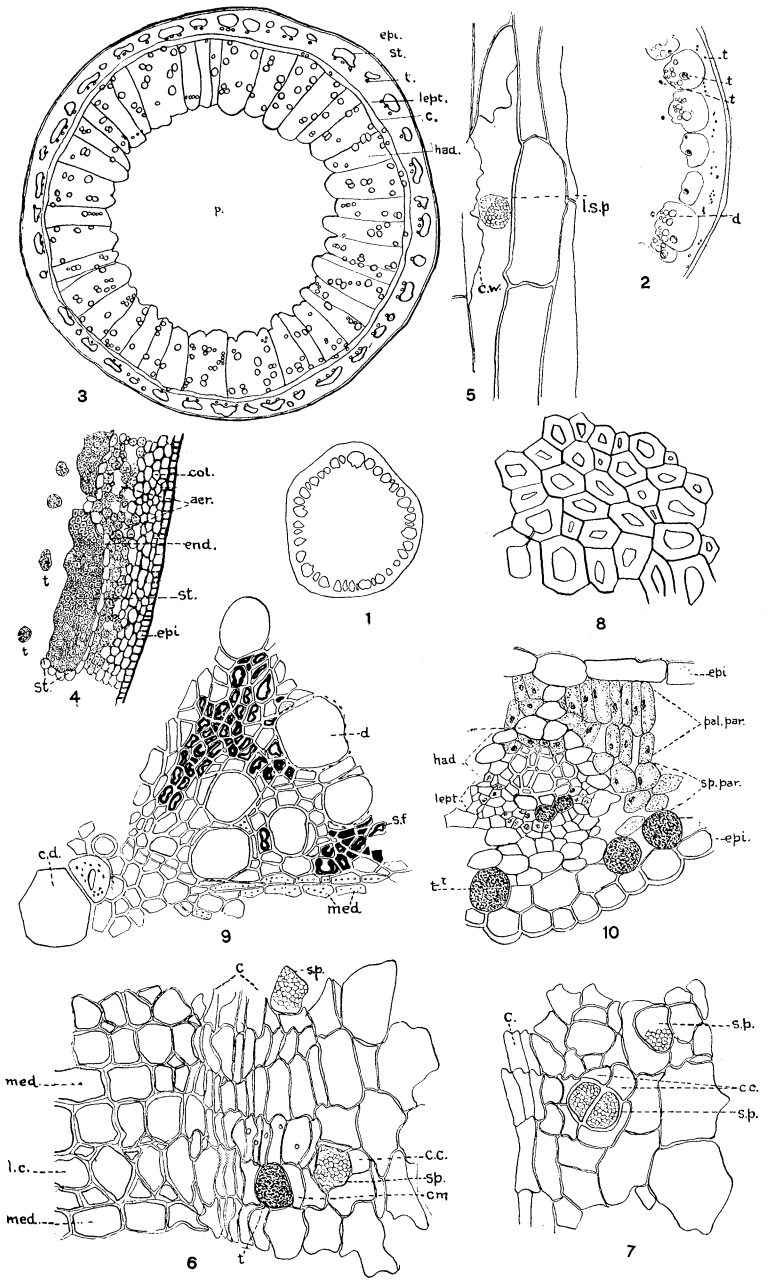
FIG. 6. Transverse section at 18 cm., showing cambium, *c*; *med*, medullary ray cells; *l. c*, libriform cells; *s. p*, sieve plates; *t*, tannin cell; *c. c*, companion cell; *c. m*, cambiform cell; × 318.

FIG. 7. Transverse section at 18 cm., showing twin sieve-plates *s, p*; *c. c*, companion cells; *c*, cambium; × 318.

FIG. 8. Transverse section at 16.7 cm., showing width of stereome walls; × 318.

FIG. Transverse section of root; *c. d*, central duct; *d*, duct; *med*, medullary ray cells; *s. f*, stereome fiber, outer wall lignified, black portion known as third membrane is of cellulose; × 318.

FIG. 10. Transverse section of leaflet near tip of the plant; *epi*, epidermis; *pal. par*, palisade tissue; *sp. par*, spongy parenchyma; *t*, tannin; *had*, hadrome; *lep*, leptome; × 318.



STABER, THE ANATOMY OF SESBAN MACROCARPA